Current Biology

Pleistocene Mitochondrial Genomes Suggest a Single Major Dispersal of Non-Africans and a Late Glacial Population Turnover in Europe

Highlights

- Newly generated pre-Neolithic European mtDNA genomes triple the number available

- Clade M found for the first time in Europe, prior to the Last Glacial Maximum bottleneck

- Rapid single dispersal of all non-Africans less than 55,000 years ago

- Previously unknown major population shift in Europe at the end of the Pleistocene

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In Brief

Posth et al. recover 35 new mitochondrial genomes from Late Pleistocene and early Holocene European hunter-gatherers. Major human mtDNA haplogroup M, absent in contemporary Europeans, is discovered in several pre-Last Glacial Maximum individuals. Demographic modeling reveals a major population turnover during the Late Glacial ~14,500 years ago.

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Pleistocene Mitochondrial Genomes Suggest a Single Major Dispersal of Non-Africans and a Late Glacial Population Turnover in Europe

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SUMMARY

How modern humans dispersed into Eurasia and Australasia, including the number of separate expansions and their timings, is highly debated [1, 2]. Two categories of models are proposed for the dispersal of non-Africans: (1) single dispersal, i.e., a single major diffusion of modern humans across Eurasia and Australasia [3–5]; and (2) multiple dispersal, i.e., additional earlier population expansions that may have contributed to the genetic diversity of some present-day humans outside of Africa [6–9]. Many variants of these models focus largely on Asia and Australasia, neglecting human dispersal into Europe, thus explaining only a subset of the entire colonization process outside of Africa [3–5, 8, 9]. The genetic diversity of the first modern humans who spread into Europe during the Late Pleistocene and the impact of subsequent climatic events on their demography are largely unknown. Here we analyze 55 complete human mitochondrial genomes (mtDNAs) of hunter-gatherers spanning ∼35,000 years of European prehistory. We

Figure 1. Late Pleistocene and Early Holocene Archeological Sites and Hunter-Gatherer mtDNA Haplogroups
(A) Pre-LGM dispersal of non-African populations, carrying both M and N lineages (hgs R, U, U5, and U2'3'4'7'8'9 belong to the N clade, distinct from the M clade).
(B) Post-LGM re-expansion in Europe while ice sheets retracted.
(C) Late Glacial shift in mtDNA hg frequency.
(D) Holocene hunter-gatherer mtDNA, mainly belonging to hg U5.
See also Table S1, Table S2, Table S4, and the Supplemental Experimental Procedures.

unexpectedly find mtDNA lineage M in individuals prior to the Last Glacial Maximum (LGM). This lineage is absent in contemporary Europeans, although it is found at high frequency in modern Asians, Australasians, and Native Americans. Dating the most recent common ancestor of each of the modern non-African mtDNA clades reveals their single, late, and rapid dispersal less than 55,000 years ago. Demographic modeling not only indicates an LGM genetic bottleneck, but also provides surprising evidence of a major population turnover in Europe around 14,500 years ago during the Late Glacial, a period of climatic instability at the end of the Pleistocene.

RESULTS AND DISCUSSION

Genetic studies of human mitochondrial DNA (mtDNA) show that all present-day non-Africans belong to two basal mtDNA haplogroups (hgs), M and N [10]. The time to the most recent com-

mon ancestor (TMRCA) of each of these two clades has been estimated independently at around 50,000 years ago (50 ka) (95% confidence interval [CI], 53–46 ka) and 59 ka (95% CI, 64–54 ka), respectively [11]. However, whereas present-day Asians, Australasians, and Native Americans carry both M and N mtDNA hgs, modern individuals with European ancestry lack almost completely lineages of the M clade [12]. The different spatial distributions and TMRCA estimates of these two ancestral clades have been interpreted as evidence of an early spread of modern humans carrying hg M into Asia, perhaps via a southern route, followed by a later non-African diffusion of the N clade, perhaps via a northern route [7]. However, an alternative model proposes a rapid and single dispersal across Eurasia, with Asia being reached first, whereas Western Eurasia would have been settled only after a hiatus, during which hg M was lost [4].

Little is known about the genetic makeup of the first European hunter-gatherers, who likely arrived ∼45 ka [13], or about the subsequent population dynamics during the nearly 40,000 years spanning from the Late Pleistocene to the Neolithic transition [14]. Here, we reconstructed 35 complete or nearly complete mtDNAs (from 11× to 1,860× average coverage) of ancient
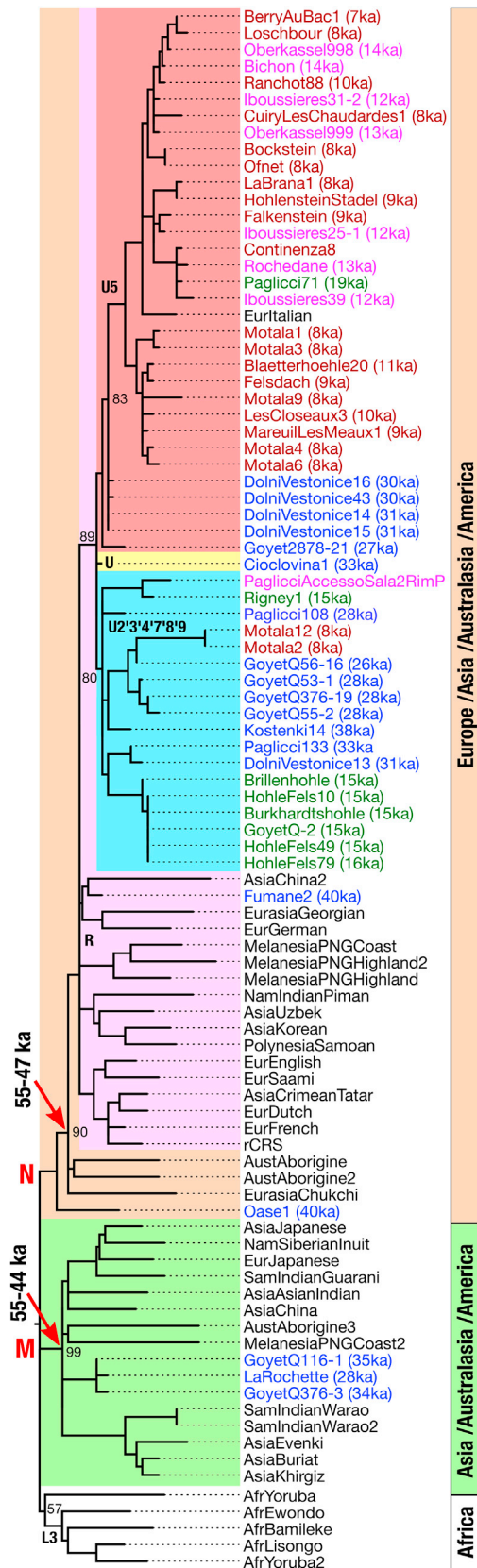
Figure 2. Maximum Parsimony Tree of Present-Day Human and 55 Pre-Neolithic mtDNA Genomes

Pre-LGM samples are shown in blue, Post-LGM in green, Late Glacial in magenta, Holocene hunter-gatherers in red, and present-day individuals in black print. Average values of ^{14}C dates are reported next to each specimen when available. Red arrows indicate divergence times of M and N clades. Hg M is almost absent in present-day individuals with European ancestry. Oase1 represents a pre-N lineage. The tree is rooted with one Neanderthal and 16 deeply divergent African mtDNAs (not shown). See also Figure S1 and the Supplemental Experimental Procedures.

modern human individuals from Italy, Germany, Belgium, France, Czech Republic, and Romania, spanning in age from 35 to 7 ka (Figure 1; Table S1). Hybridization capture of mtDNA in combination with high-throughput sequencing technologies [15] allowed us to evaluate typical DNA damage patterns and average fragment length [16] as criteria for authentication of ancient DNA (Supplemental Experimental Procedures). Both features were taken into account in an iterative probabilistic approach [17] that jointly estimates present-day human contamination and reconstructs mtDNA sequences (Table S2). Combining 311 modern and 66 ancient dated worldwide mtDNA genomes (both new and from the literature; Table S3), we used Bayesian phylogenetic methods [18] to estimate the mutation rate and hg coalescence times. Further, we combined our 35 new mtDNA genomes with 20 previously published ancient European mtDNAs for a total of 55 pre-Neolithic sequences (Table S4) and explicitly tested scenarios of the early population history of Europe using coalescent demographic modeling paired with approximate Bayesian computation (ABC) [19] (Supplemental Experimental Procedures).

Hg assignment of the authenticated mtDNAs confirmed that the vast majority of Late Pleistocene and Early Holocene individuals belonged to the U lineage, which is a subgroup of the N clade [20] (Figures 2 and S1). We also found a basal U lineage that had no derived position leading to known sub-hgs in a 33,000-year-old Romanian individual. Surprisingly, three hunter-gatherers from Belgium and France dating to between 35 and 28 ka carried mtDNA hg M, today found predominantly in Asia, Australasia, and the Americas, although it is almost absent in extant populations with European ancestry [12].

We used 66 ancient dated mtDNAs as tip calibration points in BEAST v1.8.1 [18] in combination with 311 modern worldwide mtDNA sequences to reduce the possible impact of sample biases (Table S3 and Supplemental Experimental Procedures) in estimating the mtDNA mutation rate and hg M and N divergence times. Strict and uncorrelated lognormal relaxed clocks were tested, under both a constant size and a Bayesian skyline tree prior. The four analyses returned mtDNA mutation rates (Table 1) consistent with previously published rates using similar methodology [21, 22]. The Bayesian skyline, in combination with strict rate variation among branches, performed best according to stepping-stone and path sampling methods [23] and highest effective sample size (ESS) values, giving a best estimate of the mutation rate of 2.74×10^{-8} (95% highest posterior density [HPD], 2.44–3.01×10^{-8}) mutation/site/year. This model allowed us to refine time estimates for the TMRCA of the basal non-African clades M and N of circa 49 ka (95% HPD, 54.8–43.6 ka) and 51 ka (95% HPD, 55.1–46.9 ka),

Table 1. Haplogroup Divergence Times and mtDNA Mutation Rate

Tree Prior	Clock	Statistic	Divergence Time			Log Marginal Likelihood	
			TMRCA hg M	TMRCA hg N	Clock Rate Whole mtDNA	Stepping-Stone Sampling	Path Sampling
Constant	strict	mean	58,869	57,482	2.62×10^{-8}	−48,759	−48,754
		median	58,578	57,181	2.62×10^{-8}		
		95% HPD	68,163–50,380	64,363–51,387	2.30–2.93×10^{-8}		
		ESS	585	445	651		
Constant	relaxed	mean	58,961	58,531	2.67×10^{-8}	−48,755	−48,751
		median	58,507	58,207	2.67×10^{-8}		
		95% HPD	70,389–49,125	66,398–51,664	2.30–3.04×10^{-8}		
		ESS	354	416	431		
Skyline	strict	mean	49,106	50,562	2.74×10^{-8}	−48,577	−48,571
		median	48,837	50,317	2.74×10^{-8}		
		95% HPD	54,780–43,598	55,138–46,892	2.44–3.01×10^{-8}		
		ESS	741	799	863		
Skyline	relaxed	mean	48,005	50,179	2.77×10^{-8}	−48,550	−48,546
		median	47,695	50,021	2.77×10^{-8}		
		95% HPD	53,917–43,054	54,189–46,483	2.47–3.07×10^{-8}		
		ESS	251	285	348		

The values reported are obtained in BEAST [18] using 377 worldwide mtDNAs, 66 of which come from ancient dated human remains. A Bayesian skyline tree prior in combination with strict rate variation between branches performed better than the other three tested models according to higher log marginal likelihood estimates (compared to the constant tree prior models) and effective sample size (ESS) values. HPD, highest posterior density. See also Table S3 and the Supplemental Experimental Procedures.

respectively (Table 1; Figure 2; Supplemental Experimental Procedures).

The observed mtDNA hg variation through time, including the apparent loss of hg M in Europe, suggests a genetic bottleneck that may have been influenced by climatic events (Figure 3). This period of European prehistory was accompanied by severe climatic fluctuations, such as the Last Glacial Maximum (LGM, 25 to 19.5 ka) and, at the end of the Pleistocene, the Bølling-Allerød interstadial followed by the stadial Younger Dryas—a period we refer to as the Late Glacial (14.5 to 11.5 ka) [24, 25]. These climatic changes have been proposed as a driver of the range contraction to refugia in many species [26], including modern humans, for whom there is absence of evidence of northwestern European occupation during the LGM [25, 27]. We used coalescent modeling paired with ABC [19] to test a range of explicit models of European hunter-gatherer demography (Figure S2; Table S6), using the complete set of 55 pre-Neolithic ancient mtDNA genomes (Table S4). The best-fitting model (Figure 3 and 2b in Figure S2) strongly supports maternal population continuity through the LGM, albeit as a single genetic bottleneck, before being replaced by a new incoming population at the onset of the Late Glacial 14.5 ka (model posterior probability, $P_{2b} = 0.807$). Based on the estimated parameter values of this model (Table S5), we infer that this surviving population diverged from the ancestral one around 29 ka (95% HPD, 36–25 ka), prior to the beginning of the LGM.

The new hunter-gatherer mtDNA genomes reported here approximately triple the available sequences from pre-Neolithic Europe. One novel finding, that three out of 18 European pre-LGM hunter-gatherers carry a previously undescribed basal mtDNA lineage M (Figure 1A), has important implications for the timing of the dispersal of modern humans into Eurasia.

Excluding a ~40,000-year-old Romanian individual known not to have contributed notably to the modern European gene pool [28], our BEAST analyses give a TMRCA for clades M and N from 44 to 55 ka, respectively. Our estimated dates, together with the oldest accepted archeological evidence for the presence of early modern humans in Australia and Europe (both dated to at least 45 ka [13, 29]), are consistent with a model of a single, late, and therefore rapid dispersal of a source population containing both M and N hgs, which contributed all the mitochondrial diversity of present-day non-Africans (cf. [7]). Human individuals whose ancestries trace back to potential earlier expansion(s) outside Africa [30, 31] are thus unlikely to have left any surviving mtDNA descendants.

Phylogeographic inference based solely on mtDNA has limitations [2], but information from single loci can provide meaningful constraints on models of human prehistory. In particular, the fact that hg M has never previously been found in Europe is generally interpreted as an important limitation for the proposed scenarios of non-African population dispersals [4, 7]. According to the most popular model [4], an early expansion occurred before the M and N diversification with a subsequent loss of M in only the population ancestral to Europeans. Our evidence for the existence of hg M in Late Pleistocene Europe revises this scenario. It suggests that the loss of hg M may be due to population dynamics that occurred later within Europe itself. The expansion either occurred before the diversification of M and N, with subsequent migration bringing both lineages into Europe, or the dispersal was later, occurring after their TMRCAs. Contrary to recent findings [11], though similar to a previous study [32], our two TMRCAs are almost identically dated, suggesting a single major dispersal after 55 ka for all non-African populations, including Europe. The genetic evidence of pre-LGM hg M
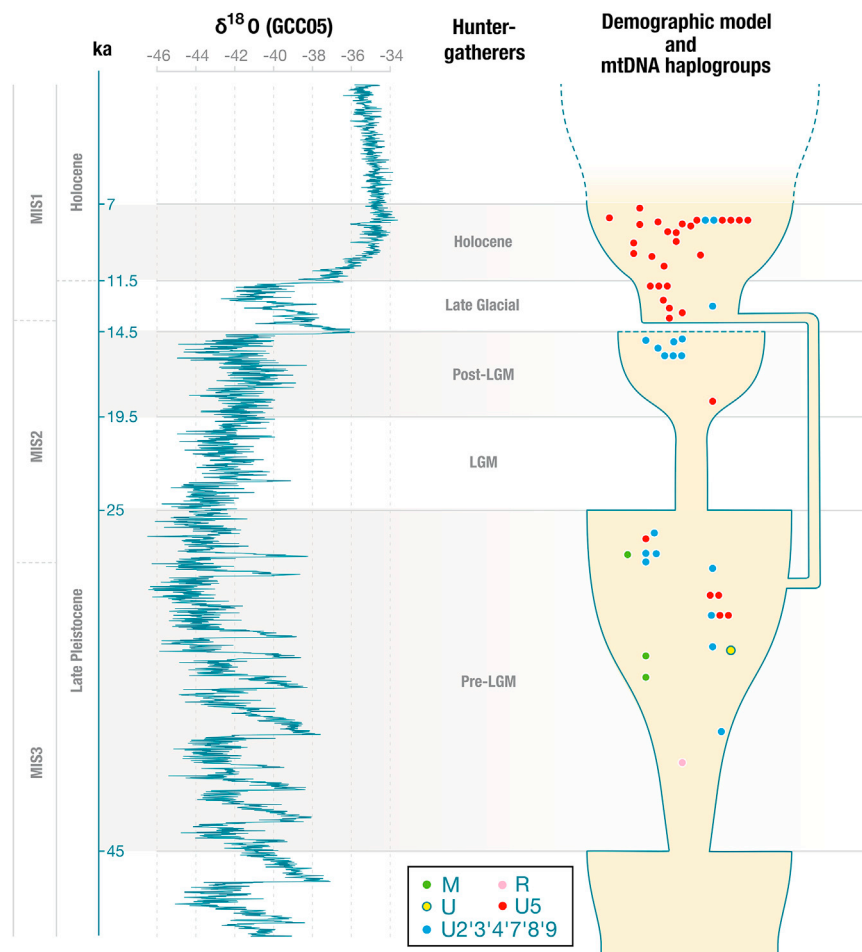
during the Bølling-Allerød interstadial and followed by a similarly drastic period of cooling during the Younger Dryas [24]. Globally, the early warming phases of the Late Glacial are strongly associated with substantial demographic changes, including extinctions of several megafaunal species [34] and the first expansion of modern humans into the Americas [35]. In European hunter-gatherers, our model best explains this period of upheaval as a replacement of the post-LGM maternal population by one from another source. Although the exact origin for this later population is unknown, the inferred demographic history (Figure 3 and 2b in Figure S2) suggests that it descended from another, separate LGM refugium. On the basis of mtDNA alone, we cannot rule out some degree of genomic continuity throughout the Late Pleistocene and early Holocene hunter-gatherer populations, and thus into present-day Europeans [14]. For this reason, we interpret our model as capturing the maternal signal of a major population shift, rather than a complete replacement. Ancient nuclear DNA data and additional geographically and temporally distributed specimens may provide a more comprehensive picture, possibly identifying the source and ancestry of these later incoming hunter-gatherers.

In conclusion, the large dataset presented here allowed us to provide a late upper bound on the major dispersal of all non-Africans and to uncover unexpected population dynamics of European hunter-gatherers. The Late Glacial event that we identify here is the oldest in an accumulating list of major European population turnovers revealed by ancient mtDNA [20].

ACCESSION NUMBERS

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indicates that this lineage reached Western Europe by at least 35 ka (GoyetQ116-1), either alongside the first arrival of N or later. The reconstructed phylogeny (Figure 2) with both basal N and M lineages in Late Pleistocene Europe possibly mirrors the inferred back migration into Africa, which has been suggested by the existence of hgs U6 and M1 in modern-day North Africans [33]. Therefore, the major modern human dispersal described here after 55 ka might have affected not only non-Africans, but also African populations to some extent.

The potential impact of climatic events on the demography, and thus the genetic diversity of early Europeans, has previously been difficult to quantify, but it likely had consequences for the relative components of ancient ancestry in modern-day populations [14]. Our demographic modeling reveals a dynamic history of hunter-gatherers, including a previously unknown major population shift during the Late Glacial interstadial (the Bølling-Allerød, ∼14.5 ka). Under our best-fitting model (Figure 3 and 2b in Figure S2), the small initial founder population of Europe slowly grows up until ∼25 ka and survives with smaller size in LGM climatic refugia (25–19.5 ka) [25] before re-expanding as the ice sheets retract (Figure 1B). Although this model supports population continuity from pre- to post-LGM, the genetic bottleneck is consistent with the apparent loss of hg M in the post-LGM. The subsequent Late Glacial period is characterized by drastic climatic fluctuations, beginning with an abrupt warming

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Update

Current Biology

Pleistocene Mitochondrial Genomes Suggest a Single Major Dispersal of Non-Africans and a Late Glacial Population Turnover in Europe

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The version of this article originally published online contained two minor graphical presentation errors, which do not affect the results or conclusions. These errors have now been corrected in the article online and will be corrected in the printed edition as well, as follows:

In Figure 1A, one individual from the Dolní Věstonice archeological site originally represented with a red point (mtDNA haplogroup U5) has been corrected to a blue point (mtDNA haplogroup U2'3'4'7'8'9).

In Figure 3, two blue points representing two contemporaneous individuals from the same location (Goyet, Belgium) were superimposed, appearing as a single point. Both points are now visibly distinct, giving a total of 55 individuals as reported in the Figure 3 legend.

The corrected and original figures are shown below for reference.

Additionally, the version originally published online contained an error in the name of author Dan Grigorescu, whose surname we misspelled as "Grigourescu." This error has now been corrected online and will be corrected in the printed edition as well.

The authors apologize for these errors.

Figure 1. Late Pleistocene and Early Holocene Archeological Sites and Hunter-Gatherer mtDNA Haplogroups (corrected)

Figure 1. Late Pleistocene and Early Holocene Archeological Sites and Hunter-Gatherer mtDNA Haplogroups (original)
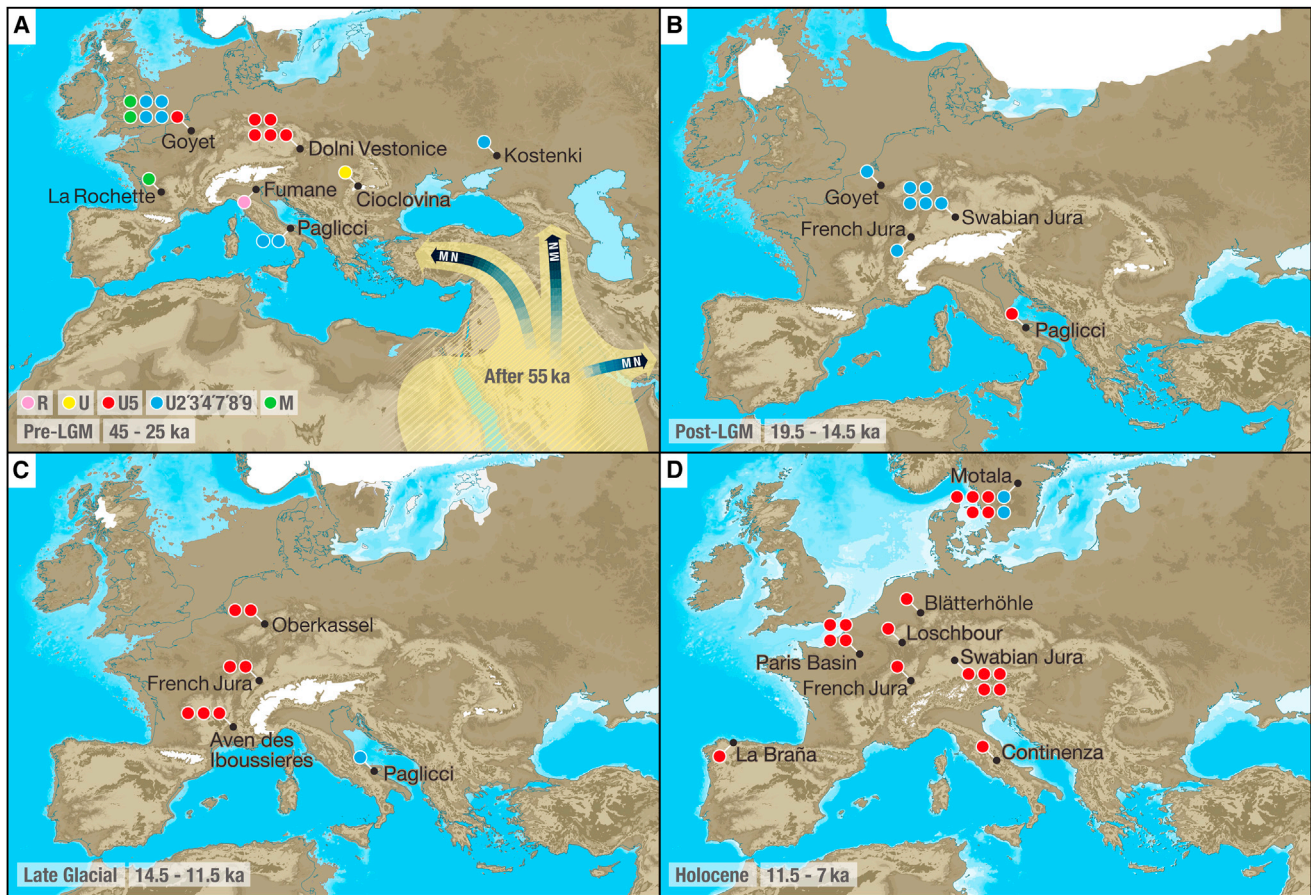
Figure 3. Late Pleistocene and Early Holocene Climatic Fluctuations and European Hunter-Gatherer Demography (corrected)
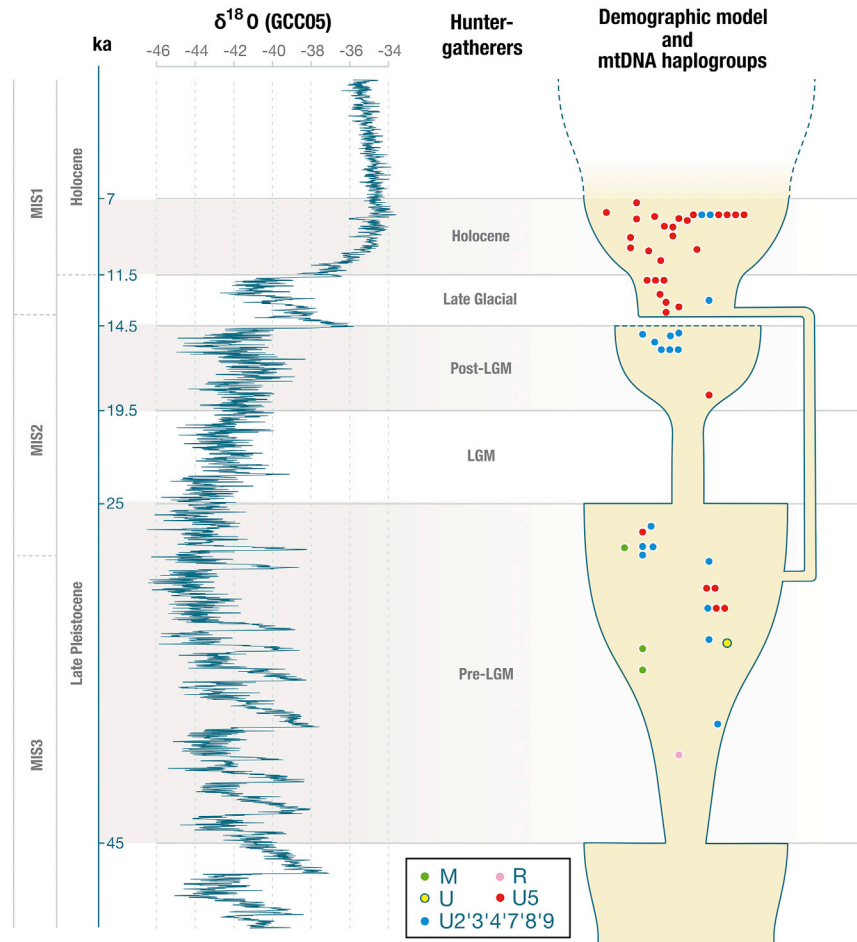
Figure 3. Late Pleistocene and Early Holocene Climatic Fluctuations and European Hunter-Gatherer Demography (original)